A COMPARISON OF FISH ASSEMBLAGES
FROM TWO TYPES OF ALGAL BEDS AND CORAL REEFS
IN THE SOUTH-WEST LAGOON OF NEW CALEDONIA

by

Olivier ROSSIER & Michel KULBICKI (1)

ABSTRACT. - Whereas fish assemblages of tropical seagrass beds have been widely studied, those of tropical macroalgal beds are poorly known. To provide information about these assemblages, the fish of two different types of algal beds (dominated by *Sargassum* sp. and *Halimeda* sp.) were sampled using visual census in the south-west lagoon of New Caledonia, and were compared to coral reefs. The number of species present on *Sargassum* beds (202 spp.) and reefs (187 spp.) was more than twice that observed on *Halimeda* beds (86 spp.). Only 42 species were shared among the three habitat types. Mean species richness and density decreased sharply from reefs (52 species per transect, 6 fish / m²) to *Sargassum* (35, 1.5) and *Halimeda* beds (11.5, 0.2). Differences between the two algal beds probably resulted from the higher structural complexity of the *Sargassum* beds (presence of a higher coral, rocky and algal cover than in *Halimeda* beds). Pomacentridae greatly dominated fish assemblages on reefs and *Sargassum* beds whereas Lethrinidae were prevailing on *Halimeda* beds. Important similarities were observed between the dominant species from reefs and *Sargassum* beds (e.g., *Neopomacentrus* spp., *Pomacentrus moluccensis*, *Scolopsis bilineatus*), whereas major differences existed with *Halimeda* beds on which *Lethrinus genivittatus* was dominant. Species diversity among trophic categories was relatively similar between habitat types but the density and the biomass varied markedly, especially between *Halimeda* beds and the two other habitats. Territorial or sedentary fishes were dominant on reefs whereas a higher proportion of the large roaming fishes was found on algal beds. This study gives a useful description of the poorly known fish assemblages in tropical algal beds and demonstrates that different algal habitats support different fish assemblages.

RÉSUMÉ. - Comparaison des communautés de poissons de deux types de champs de macrophytes et de récifs coralliens dans le lagon sud-ouest de Nouvelle-Calédonie.

Alors que les communautés de poissons des herbiers marins tropicaux ont été bien étudiées, celles des champs de macrophytes sont mal connues. Pour combler cette lacune, les poissons de deux types de champs de macrophytes (dominés respectivement par des *Halimeda* et des *Sargassum*) ont été échantillonnés par comptages en plongée dans le lagon sud-ouest de Nouvelle Calédonie. Ces communautés ont ensuite été comparées à celles des récifs. Le nombre d'espèces présentes dans les *Sargassum* (202 spp.) et sur les récifs (187 spp.) est plus du double du nombre observé dans les *Halimeda* (86 spp.). Les trois habitats n'ont que 42 espèces communes. La richesse spécifique moyenne et la densité diminuent rapidement des récifs (52 espèces /transect, 6 poissons/m²) aux *Sargassum* (35, 1.5) et aux *Halimeda* (11.5, 0.2). Les différences entre les deux types d'algueraies sont probablement le résultat d'une plus grande complexité du substrat (couvertures algale, corallienne et rocheuse supérieures) dans les *Sargassum* que dans les *Halimeda*. Les Pomacentridae sont prépondérants dans les communautés récifales et de *Sargassum*, tandis que les Lethrinidae dominent dans les *Halimeda*. Des similarités importantes existent dans la composition des espèces dominantes entre récifs et *Sargassum* (par ex. *Neopomacentrus* spp., *Pomacentrus moluccensis*, *Scolopsis bilineatus*), tandis que des différences majeures existaient avec les *Halimeda* sur lesquelles *Lethrinus genivittatus* domine. La diversité spécifique parmi les catégories trophiques est relativement similaire entre les habitats. En revanche, la densité

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(1) IRD, Centre de Nouméa, BP A5, 98848 Nouméa Cedex, NOUVELLE-CALÉDONIE.
[kulbicki@noumea.ird.nc]

et la biomasse des communautés dans les *Halimeda* diffèrent significativement de celles des récifs et dans les *Sargassum*. Les espèces territoriales ou sédentaires dominent sur les récifs alors que la proportion des espèces mobiles augmente dans les champs d'algues. Cette étude donne une description utile de communautés de poissons jusqu'à présent mal connues et démontre que suivant le type d'algues, les communautés diffèrent.

Key words. - Fish assemblages - ISEW - New Caledonia - Algal bed - Coral reef.

Tropical shallow waters encompass diverse habitat types including coral reef, bare sand, seagrass beds or mangroves which support different fish assemblages (Blaber *et al.*, 1985; Robertson and Duke, 1987; Thollot and Kulbicki, 1988; Sedberry and Carter, 1993) which interact with one another (Parrish, 1989). In addition to coral reefs which have been extensively studied (cf. Sale, 1991), special attention has been given to seagrass beds (Weinstein and Heck, 1979; Martin and Cooper, 1981; Harmelin-Vivien, 1983; Baelde, 1990 among others) probably because these areas are known to be important nurseries for many fish species as well in tropical areas (Jones and Chase, 1975; Pollard, 1984; Blaber *et al.*, 1992) as in temperate regions (Hannan and Williams, 1998; Levin *et al.*, 1997; Francour, 1997).

In the lagoon of New Caledonia, seagrass beds are widely present but other vegetated habitats, macroalgal beds, occur in many places and may cover extensive zones in the south-west lagoon (Garrigue, 1985, 1995). Previous observations (Kulbicki unpubl. data) suggested that, like seagrass beds, these habitats could play an important role for fish. Unfortunately, whereas several studies have demonstrated the influence of macroalgae on fish recruitment (Jones, 1984; Carr, 1991; Levin, 1993) and adult abundance (Choat and Ayling, 1987; Anderson, 1994; Levin and Hay, 1996) on temperate reefs, no studies have focused on fish assemblages associated with algal habitats in tropical lagoons.

Thus, the primary goal of this paper is to describe the organisation of the fish assemblages found on algal beds in the tropical Pacific. The second purpose is to test the independence of these assemblages with those of nearby reefs. In particular, we want to know if similar species or functional groups are found in both habitats and what may be the reasons and consequences for observed differences.

MATERIAL AND METHODS

Site selection

Between 1985 and 1990, the fish community, benthos and substratum were sampled over more than 400 stations in the South-West lagoon of New Caledonia. These stations included a large variety of habitat types such as coral reef, bare sand, mud flat, seagrass bed or algal bed. From these stations we selected those in which homogeneous algal beds occurred (i.e., with few other covers such as coral reef) independent of sampling period (i.e., some stations were sampled in 1986 others in 1990). Because two major types of algal assemblages existed in our dataset, the stations were separated into two groups according to algal composition. *Sargassum* sp. and *Lobophora* sp. were the main species found in the first assemblage (20 samples) whereas *Halimeda* sp. and *Caulerpa* sp.
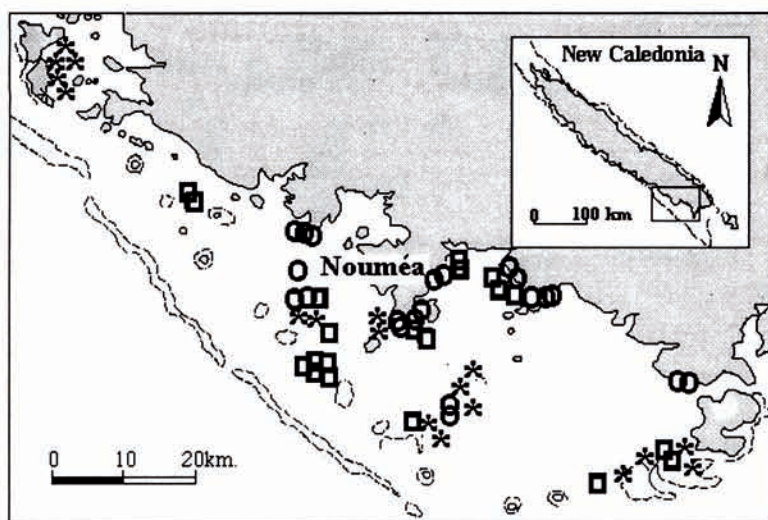
Fig. 1. - Location of the sampling stations in the South-West lagoon of New Caledonia. ○: coral reefs;.
▢: *Sargassum* beds; *: *Halimeda* beds.

characterised the second group (18 samples). Other algae or seagrasses such as *Halodule* sp. or *Halophila* sp. were occasionally present.

       To compare the fish assemblages in algal beds with coral reefs, we selected 20 randomly chosen stations in coral reef habitat. Location of the sampling stations is given on figure 1.

Sampling

       Fish were recorded by visual census along 100 m long transects, the start of each transect being chosen at random. The transects were laid parallel to the slope. Two divers, one on each side of the transect line, separately recorded all fish on each side of the transect. Cryptic species and newly recruited fish less than 5 cm long, were not recorded. For each record, the species name, number of fish observed, size of fish and the perpendicular distance of fish to the transect were noted.

       The sizes of all fish were estimated. The accuracy of fish size estimate was not tested during this experiment. However, it is now admitted that errors are at most 20% and usually well below 10%. The estimation of sizes underwater is usually accurate if the divers have some training (Bell *et al.*, 1985; Harmelin-Vivien *et al.*, 1985; Kulbicki, 1988, 1995; Kulbicki and Wantiez, 1990; St John *et al.*, 1990). However, lengths of some species tend to be underestimated (elongated fish such as Fistularidae, Aulostomidae, Belonidae) and lengths of others overestimated (round fish such as Chaetodontidae, Acanthuridae, Siganidae) (Kulbicki *et al.*, 1994). Errors in size estimates also tend to increase as size increases. Therefore, the size classes of our estimates were broadened with size as recommended by Bell *et al.* (1985): 1 cm classes for fish less than 10 cm, 2 cm classes for fish between 10 and 30 cm, 5 cm classes for fish between 30 and 50 cm and 10 cm classes for fish more than 50 cm.

       The distance from each fish to the transect line was estimated in 1 m classes up to 5 m and in 2 m classes for greater distances. Fish beyond 12 m from the transect were

not counted. Densities were calculated according to distance sampling methods given by Burnham *et al.* (1980) and Buckland *et al.* (1993) and detailed in Wantiez *et al.* (1997). Distance sampling was preferred over strip transects as the former yields more accurate (Ensign *et al.*, 1995) and less biased (Kulbicki, 1998) results for underwater visual censuses. Fish weights were estimated from length-weight relationships (Kulbicki *et al.*, 1993a; Letourneur *et al.*, 1998). Biomasses were estimated using these fish weights and the same method as for densities. The distance of the fish to the transect was estimated visually and not measured. Studies which have investigated the estimation of distances by divers give diverging opinions. Thresher and Gunn (1986) found important differences in distance estimates between divers, while Bohnsack and Bannerot (1986) indicated that with practice a diver could estimate a distance of 7.5 m within 0.5 m. Nolan and Taylor (1980) found that divers were able to estimate a 5 m distance within 0.5 m and that with training divers could be accurate to within 0.2 m. In a study involving estimates from 10 different divers (Kulbicki, 1998), the distance estimates were statistically different for only one diver (who was not using the method properly). It is therefore likely that there was some error on the distance estimates. However, the magnitude of this error should be similar within the three habitats tested and were of little consequences when comparing density or biomass estimates. In addition, most fish were observed at short range, where errors on distance would have been minimal.

The diet of each fish species was either taken from the data used by Kulbicki *et al.* (1994), from the database FISHEYE (Labrosse *et al.*, 1998) or from the information in FISHBASE (Froese and Pauly, 1998). Species with no direct information available were assigned the same diet as the closest species for which information was available. The food items were divided into 9 categories: fish, macroinvertebrates, microinvertebrates, zooplankton, other plankton, macroalgae, microalgae, coral, detritus. The percentage of each of these food items in a species' diet was taken into account when calculating the contribution of that species to a trophic category.

Species were also classified by ecological group (i.e., territorial, sedentary, small radius roaming, and large radius roaming) to compare the relative contributions each of these groups of species made to species composition, density and biomass in the different habitats.

On each transect, the substratum composition as well as algal and coral cover were visually recorded whithin a 5 m wide strip, according to the method used by Kulbicki *et al.* (1993b). A comparison with point intercept methods (Garrigue and Kulbicki, unpubl. data, 1996) indicated that differences in algae or coral cover were less than 10%.

Data analysis

The Jaccard coefficient of similarity (based on presence/absence of species, with double zeros omitted) was used to compare species composition among samples. Cluster analysis using Ward's method of amalgamation (Ward, 1963) was then conducted to group stations according to their species composition. Rare species (those occurring in less than 3 samples) and undetermined fish (i.e., *Scarus* sp.) were excluded from the analysis. Similar cluster analyses were performed using Ward's method and Euclidian distances on standardised data of density and biomass. For these latter analyses, only species occuring in at least two habitats were considered.

Mean species richness, total abundance and biomass among reefs, *Sargassum* beds and *Halimeda* beds were compared using one-way ANOVA and the Scheffe test. For this analysis, abundance and biomass were $\ln(x+1)$ transformed. Because several datasets were

not normally distributed even after transformation, family abundance and biomass between habitats were compared using non-parametric Kruskal-Wallis test. If this test was significant, pairwise habitat comparisons were made using the Mann-Whitney U-test.

Pearson's correlation coefficient between ichthyofaunal data (species richness, total abundance and biomass) and substratum variables (% of rocky substrate, coral and algal cover) were calculated within habitats to test for significance between these factors.

To determine the dominant families and species of the different habitat types, each fish family and species was ranked according to its importance in the community in terms of frequency of occurrence, total abundance and biomass. These ranks were summed to produce an overall rank of importance or "dominance index" (Burchmore et al., 1984).

χ^2 tests were realised to analyse differences in trophic or mobility structures between habitats. Variations with habitat of the relationships between trophic and mobility structures and environmental variables (coral and algal covers, hard substratum cover) were tested at the general level (all groups pooled) with MANOVAs and at the group level with covariance analyses.

RESULTS

Habitat   description

All the environmental parameters tested (depth, coral, algal and hard substrate covers) were significantly different between reefs, *Sargassum* beds and *Halimeda* beds (Table I). Reefs were shallow (2.58 m ± 0.15),   had large coral (48.35% ± 4.29)   and hard substrate (65.25% ± 4.98) covers but low algal cover (2.4% ± 0.36). *Sargassum*

Table I. - Characteristics of the groups defined by habitats and the clusters on figures 2A, B, C. Variables followed by (nb) indicate number of stations in a category.

		Habitats			Cluster species		Cluster density				Cluster biomass		
	Groups	Reef	Sarg	Hal	1	2	1	2	3	4	1	2	3
Habitat	Reef (nb)	20	0	0	20	0	3	14	1	2	0	15	5
	Sargassum (nb)	0	20	0	7	13	4	6	3	7	10	6	4
	Halimeda (nb)	0	0	18	0	18	0	0	4	14	18	0	0
Substratum	%Hard substratum	65.2	34.7	3.6	65.7	9.3	44.3	69.8	13.0	11.0	9.5	65.5	46.7
	%Coral	48.3	9.3	1.7	41.2	2.3	33.1	39.0	9.7	4.0	2.2	40.0	31.3
	%Algae	2.4	40.1	26.8	8.9	35.3	19.5	9.8	43.6	28.3	33.6	11.9	15.6
	Turbidity (m)	6.4	8.5	7.3	6.9	7.7	9.1	6.3	8.5	7.3	7.6	9.0	8.9
	Depth (m)	2.6	5.1	11.5	2.9	9.1	3.1	2.7	6.6	10.1	9.8	2.7	3.1
	Distance coast	0.4	3.1	2.9	0.8	3.2	3.6	0.3	4.1	2.5	3.1	0.5	2.7
Expos	Windward (nb)	10	4	5	13	6	2	10	1	6	6	11	2
	Leeward (nb)	10	16	13	14	25	5	10	7	17	22	10	7
Period	<1987 (nb)	2	10	16	3	26	2	0	7	19	23	1	4
	>1987 (nb)	18	10	2	24	5	5	20	1	4	5	20	5

beds were deeper than reefs (5.07 m ± 0.75) and had a much larger algal cover (40.1% ± 1.42) but showed lower hard substrate (34.7% ± 6.72) or coral cover (9.3% ± 3.01). *Halimeda* beds were the deepest (11.5 m ± 0.72) and had the lowest coral (1.67% ± 0.47) and hard substrate (3.56% ± 1.42) covers, the algal cover being intermediate between reefs and *Sargassum* beds (28.6% ± 4.45). There were also differences in the year of sampling, *Halimeda* beds samples dating from 1985-86 and reefs from 1988-90. Reefs were significantly closer to the coast than both types of algal beds. The latter were more often on the leeward sides of islands than reefs which were evenly distributed between leeward and windward expositions.

General habitat comparison

A total of 271 fish species, distributed among 48 families, was recorded in the three habitat types. Labridae (wrasses, 40 species), Pomacentridae (damselfishes, 41 sp.), Chaetodontidae (butterflyfishes, 23 sp.) and Serranidae (fairy basslets and groupers, 20 sp.) were the most speciose families. The number of species present on *Sargassum* beds (202 sp., 38 families) or reefs (187 sp., 37 families) was more than twice those observed on *Halimeda* beds (86 sp., 29 families). Only 42 species were shared among the three habitat types (Table II). There was a shift in species shared exclusively by two habitats, reefs and *Sargassum* beds having 96 species in common which were not found in *Halimeda* beds, whilst *Sargassum* and *Halimeda* beds shared only 22 such species, reefs and *Halimeda* beds having only one such species (Table II). A total of 111 species were observed exclusively in one habitat but most of these were very scarce (Table II).

Species occurrence was generally low since 63%, 78% and 89% of the species present on reefs, *Sargassum* beds and *Halimeda* beds respectively, were observed in less than

Type of species	Habitat		
	Coral reefs	*Sargassum* beds	*Halimeda* beds
Exclusive species	48	42	21
Species shared exclusively by two habitats	96 1	96 22	22 1
Species common to all habitats	42	42	42
Total species	187	202	86

Table II. - Number of species found on coral reefs, *Sargassum* beds and *Halimeda* beds.

Table III. - Mean species richness, density and biomass (min-max) of fishes recorded by visual census on coral reefs, *Sargassum* and *Halimeda* beds of the South-West lagoon of New-Caledonia. For each row, means with the same letters (a, b, c) are not significantly different at p = 0.05 (Scheffe's test).

	Reefs (n = 20)	*Sargassum* beds (n = 20)	*Halimeda* beds (n = 18)
Species richness (species/transect)	51.65a (30 - 63)	35.1b (5 - 64)	11.56c (4 - 22)
Density (fish/m^2)	6.05a (1.3 - 26.5)	1.51b (0.05 - 4.5)	0.21c (0.03 - 0.46)
Biomass (g/m^2)	103.5a (25.2 - 450.2)	63.75a (1.4 - 345.4)	10.36b (0.45 - 51.6)

25% of the transects. Reef was the only habitat where some species (9%) occurred in more than 75% of the samples.

Mean species richness and density decreased sharply from reefs (52 species per transect, 6 fish/m^2) to *Sargassum* (35, 1.5) and *Halimeda* beds (11.5, 0.2). In each case, differences between habitats were significant (Table III). Mean biomass was significantly lower on *Halimeda* beds than in the other two habitats but no differences occurred between reefs and *Sargassum* beds.
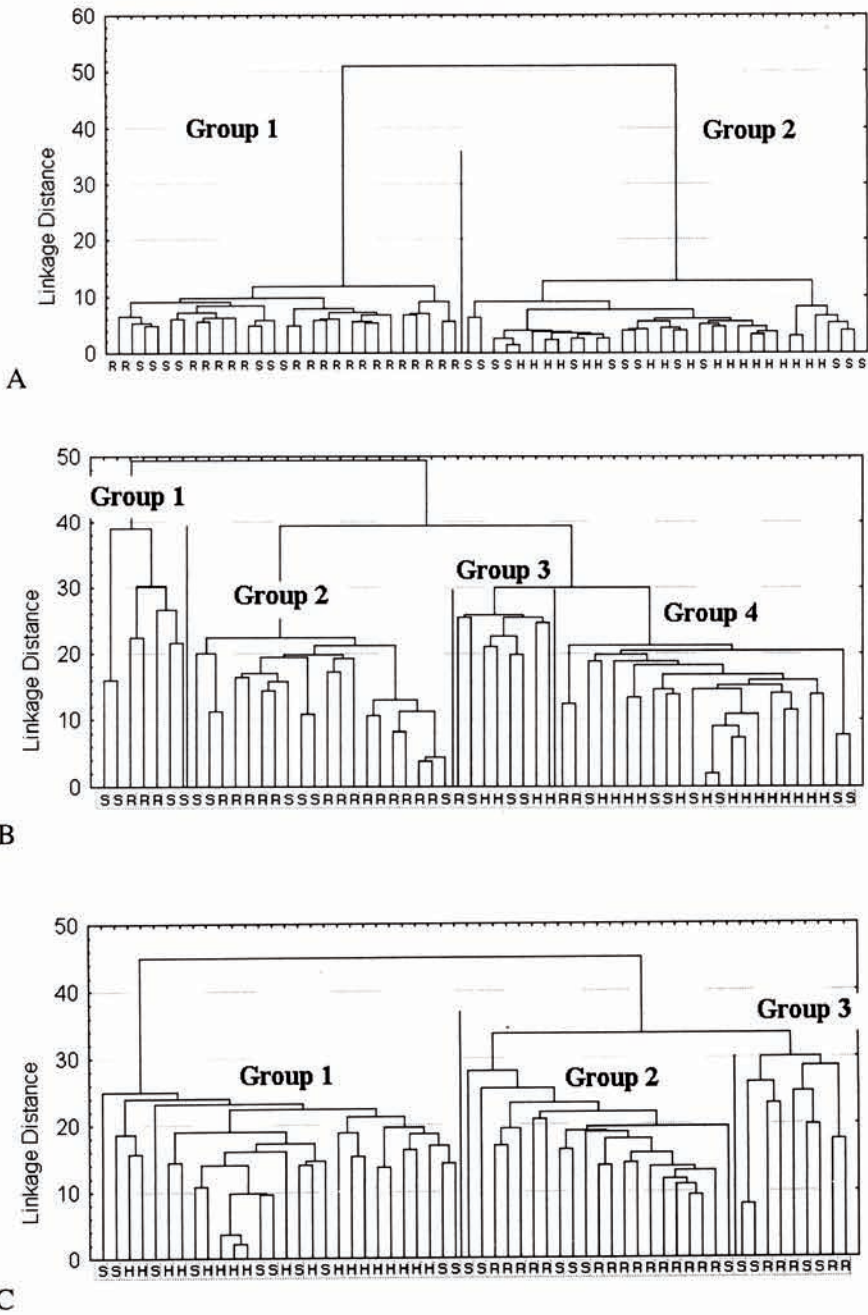
Species structure

The three cluster analyses which were performed respectively on presence/absence (Fig. 2A), density (Fig. 2B) and biomass (Fig. 2C) indicate that the data are strongly structured by species. In other words, the species composition of the stations allows a good separation of these stations into a low number of groups, respectively 2 for species, 3 for biomass and 4 for density. These groups were analysed for differences in their environmental and physical parameters (Table I). The differences between groups reflect the separation between reefs and algal beds in general, in each cluster analysis one group being dominated by reef stations (group 1 on Fig. 2A; group 2 on Fig. 2B and 2C). *Sargassum* beds were more often found among groups with reefs than groups with *Halimeda*, thus showing that this habitat supported fish assemblages which composition was closer to those from reefs than from *Halimeda* beds.

The next question was to know if once the habitat effect was taken out of these clusterings, what could be the effects of the other variables on species composition. Two types of analyses were performed on the density and biomass of each of the 161 species found in at least 2 habitats. For discrete variables (period and exposition) a two way ANOVA was performed and for continuous variables (depth, hard substrate cover, coral cover, algae cover, distance to coast and turbidity) a covariance analysis was performed with habitat as the cofactor. Only twenty species were affected by the interaction of these factors with habitat (Table IV). The contribution of these species to total density was between 0 and 39% and to total biomass between 0 and 18%. However, a large proportion of these species have a short life span and were therefore replaced through time by similar species. In particular, *Neopomacentrus nemurus* and *Chromis viridis* were often replaced by *Pomacentrus smithi*, the latter species not being affected by interactions between habitat and the other factors tested. The factor which interacted the most with habitat at the species level was coral cover. Four factors, depth, algae cover, distance to the coast and turbidity, had approximatively the same level of effect. Two factors, hard substratum cover and year had little effect on the variation of species composition within an habitat.

Correlations with environmental variables

In this paragraph only the general correlation of overall species richness, density and biomass with the factors given in table IV are considered. As these factors may interact, multiple regression analyses were performed using a stepwise procedure in order to rank the contribution of these various factors (Table V). Densities and biomasses were log transformed so as to obtain normality. The major finding is that overall species richness, density and biomass were primarily determined by hard substratum cover (Table V). Habitat and algal cover were the only other important factors in these multiple regressions. Within habitats, significant correlations were found between species richness and density with hard substratum and coral cover in *Sargassum* beds and between species richness and coral cover in *Halimeda* beds.

Fig. 2. - Clustering (Ward's method) of all samples taken on reefs (R), *Sargassum* beds (S) and *Halimeda* beds (H). **A**: Species Jaccard coefficient of similarity (58 stations × 152 species); **B**: Standardised density (58 stations x 161 species); **C**: Standardised biomass (58 stations × 161 species).

Composition of fish assemblages

Pomacentridae greatly dominated fish assemblages on reefs and *Sargassum* beds and ranked second after Lethrinidae on *Halimeda* beds (Table VI). In each habitat type, Pomacentridae was the most abundant family and represented 86% of the total density on reefs, decreasing to 59% in *Sargassum* beds and 41% in *Halimeda* beds. This family was also the major contributor to the biomass on reefs, ranked third on *Sargassum* beds (after Acanthuridae) but was only sixth on *Halimeda* beds. Pomacentridae abundance and biomass were clearly higher on reefs than on the two other habitats (Table VI) and this family was the major contributor to the density differences observed between reefs and *Sargassum* beds (Scheffe test, p > 0.05 if Pomacentridae were excluded).

With the exception of Pomacentridae, the structure of fish assemblages varied highly among the three habitat types (Table VI). On *Halimeda* beds, Lethrinidae, Mulli-

Table IV. - Contribution (%) to total density or biomass of the species which were significantly affected by both habitat and another factor. Factors analysed by an ANOVA are marked by ++, those analysed by an analysis of covariance by +. Short lived species are indicated in bold. D: density B: biomass.

Species	Depth +		% Hard substr. +		% Coral +		% Algae +		Distance to coast +		Turbidity +		Expo. ++		Year ++	
	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B
Lutjanus fulviflamma																1.4
Lutjanus quinquelineatus						2.3									0.7	2.3
Lethrinus nebulosus	0.6															
Lethrinus genivitatus					5.2		5.2		5.2		5.2					
Scolopsis bilineatus								3.1	0.9	3.1	0.9					
Abudefduf sexfasciatus					2.2	1.3	2.2		2.2	1.3	2.2					1.3
Abudefduf whitleyi								2.0						2.0		
Chromis viridis					6.1	1.3									6.1	1.3
Neopomacentrus nemurus	19.8	7.9			20.0	7.9		7.9	20	7.9	20.0	7.9			20.0	
Pomacentrus philippinus									3.3							
Pomacentrus amboinensis					5.7		5.7									
Anampses sp.	0.7						0.7									
Choerodon graphicus						2.1						2.1				
Scarus rivulatus											3.3	3.3	3.3			
Parapercis cylindrica															1.2	
Acanthurus dussumieri		3		3		3					3.0	3.0				
Acanthurus blochii								1.2				1.2				
Acanthurus nigrofuscus		1.5						1.5	0.8	1.5	1.5	1.5		1.5	.	1.5
Siganus doliatus		1.3						1.3		1.3	1.3	1.3				
Pseudobalistes fuscus													0.3			
Total	21.0	14	0	3	39.0	18	14.0	17.0	32	21.0	28.0	20.0	0.3	6.8	28.0	7.8
Short lived species	19.8	7.9			31.3	9.2	5.2	7.9	25	7.9	25.0	7.9			21.0	1.3

dae and Serranidae were prevailing families (rank 1, 3 and 4). However, Mullidae and Serranidae tended to have higher biomasses on *Sargassum* beds and reefs. Conversely, the rank of Siganidae and Acanthuridae was lower on *Halimeda* beds than on the other habitats and the abundance and biomass of several families (Nemipteridae, Chaetodontidae, Pomacentridae, Labridae, Scaridae, Acanthuridae and Siganidae) was significantly lower than on reefs and *Sargassum* (Table VI). On *Sargassum* beds families had usually biomass values which were intermediate between those of reefs and *Halimeda* beds. Fish assemblages in *Sargassum* beds differed from the other habitats mainly by the importance of Scaridae and Caesionidae (ranked 2 and 5 respectively) although these families were very patchily distributed among *Sargassum* samples. Abundance and biomass of Nemipteridae and Chaetodontidae were significantly higher on reefs than on *Sargassum* and *Halimeda* beds.

Several of the dominant species were similar in abundance on reefs and *Sargassum* beds whereas major differences existed between *Halimeda* beds and the other two habitats (Table VII). Species such as *Neopomacentrus* sp., *Pomacentrus moluccensis*, *Scolopsis bilineatus*, *Abudefduf sexfasciatus* or *Acanthurus nigrofuscus* which predominated on reefs and in *Sargassum* beds were absent or very scarce in *Halimeda* beds. Conversely, the relative abundances of *Lethrinus genivittatus*, *Upeneus* sp.1, *U. tragula* and *Parapercis cylindrica* was high in *Halimeda* beds but was low in the two other habitats. *Chromis viridis* and *Siganus doliatus* were typical species of reef fish assemblages whereas *Acanthurus dussumieri* was especially present in *Sargassum* beds.

Trophic structure of fish assemblages

A χ^2 analysis of the trophic structure (Table VIII) indicates that there were no significant differences in the proportion of the various trophic groups (Table IX) between reef and *Sargassum* beds fish assemblages, whether species richness, density or biomass are considered (Tables X, XI, XII). On the opposite, there were significant differences between reefs and *Halimeda* beds (Table VIII) for species richness, density and biomass, and significant differences between *Sargassum* beds and *Halimeda* beds for density and biomass (Table VIII). Differences between reefs and *Halimeda* beds were due to coral feeders (Reef > *Halimeda*), piscivores and macrocarnivores (*Halimeda* > Reef) for species richness, macrocarnivores (*Halimeda* > Reef) for density and macrocarnivores (*Halimeda* > Reef), plankton feeders and microherbivores (Reef > *Halimeda*) for bio-

Table V. - Results of multiple regression analyses between species richness, density and biomass with environmental factors. Empty cases indicate that the factor was not retained by the analysis. Depth, year and exposition never entered in the models (not significant) and are therefore not displayed. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

	Species richness			Log. density			Log. biomass		
	Rank	Partial r	r2	Rank	Partial r	r2	Rank	Partial r	r2
Hard substratum	1	0.39**	0.74	1	0.58***	0.72	1	0.49***	0.57
Coral cover				4	-0.31*	0.71			
Algae cover				3	-0.35**	0.43			
Distance to coast	2	0.32*	0.40						
Turbidity	3	0.30*	0.26						
Habitat				2	-0.43**	0.68			
Total r2			0.77			0.74			0.63

mass. Differences between *Sargassum* beds and *Halimeda* beds were due to the same trophic groups.

The overall effect of environmental variables on trophic structures were tested using MANOVAs. They indicate that the only overall effects on trophic structures were due to hard substratum cover at the species level and algal cover at the biomass level. In other words, for a given level of hard substratum the trophic structure was different between habitats at the species level. Similarly, for a given level of algae cover, the trophic structure was different between habitats at the biomass level. On the opposite, for a given coral cover level, no difference could be found between habitats in their trophic structures. No effect of year, distance to coast or depth on trophic structure was found when habitat was taken into account.

Table VI. - Mean density and biomass, SD in brackets, of the 10 most important families (overall rank index) on coral reefs (R), *Sargassum* beds (S) and *Halimeda* beds (H) habitats. For each family, means with different letters are significantly different at p = 0.05 (Mann-Whithney U-test performed only if Kruskall-Wallis test between the three habitat types was significant). First 10 families are those dominant on reefs. Next two families are those in the 10 dominant on *Sargassum* not included in the first 10 families and final two families those dominant on *Halimeda* not included previously.

Family	Density (fish/m^2)			Biomass (g/m^2)			Rank (m^2)		
	R (n = 20)	S (n = 20)	H (n = 18)	R (n = 20)	S (n = 20)	H (n = 18)	R	S	H
Pomacentridae	5.229a (6.363)	0.891b (1.214)	0.087c (0.107)	28.75a (33.66)	7.86b (9.79)	0.62c (0.98)	1	1	2
Chaetodontidae	0.091a (0.050)	0.018b (0.021)	0.002c (0.003)	3.43a (5.04)	0.87b (0.89)	0.3c (0.74)	2.5	7	9.5
Labridae	0.087a (0.051)	0.068a (0.067)	0.007b (0.009)	8.27a (13.39)	8.45a (10.91)	0.15b (0.24)	2.5	4	5
Lutjanidae	0.126a (0.399)	0.051a.b (0.136)	0.002b (0.006)	18.43a (53.29)	4.53a.b (11.72)	1.57b (5.68)	4	9	6
Acanthuridae	0.058a (0.044)	0.033b (0.044)	<0.001c (0.001)	6.08a (5.66)	8.08a (11.99)	0.12b (0.36)	5	3	18
Scaridae	0.057a (0.058)	0.066a (0.142)	0.002b (0.004)	6.75a (8.69)	7.29a (10.97)	0.64b (1.87)	6	2	9.5
Nemipteridae	0.049a (0.048)	0.023b (0.046)	0.001c (0.005)	14.02a (37.5)	1.72b (3.15)	0.06c (0.24)	7	11	19
Siganidae	0.033a (0.035)	0.023a (0.034)	0.001b (0.002)	2.96a (3.63)	3.47a (7.19)	0.03b (0.10)	8	6	20
Mullidae	0.008 (0.007)	0.009 (0.011)	0.018 (0.042)	1.43a (1.41)	2.03a (3.26)	0.72b (1.90)	9	8	3
Serranidae	0.011a (0.012)	0.005b (0.005)	0.004b (0.010)	2.51 (3.3)	3.13 (6.55)	1.10 (1.69)	10	13	4
Caesionidae	0.011 (0.046)	0.141 (0.59)	0.009 (0.023)	1.02 (4.47)	7.58 (31.57)	0.20 (0.48)	17	5	11
Apogonidae	0.084 (0.055)	0.132 (0.065)	0.020 (0.048)	0.45 (0.22)	1.27 (0.60)	0.13 (0.40)	11	10	7
Lethrinidae	0.002 (0.003)	0.009 (0.015)	0.034 (0.06)	0.13a (0.24)	1.53b (3.04)	1.14a.b (1.64)	18	12	1
Gobiidae	0.078 (0.222)	0.009 (0.018)	0.008 (0.020)	0.6a (0.63)	0.13a (0.26)	0.26a (0.65)	13	19	8
Other families	0.126	0.033	0.015	8.67	5.81	3.62			
Total	6.050	1.510	0.210	103.50	63.75	10.36			

The covariance analyses indicate that only few significant differences exist between habitats in the relationships between trophic groups and the environmental variables (Tables X, XI, XII). Thus for instance, coral feeders and detritus feeders had different relationships (means and/or regression coefficients) with hard substratum cover and coral cover when habitat is taken into account at the species level (Table X). An interesting fact is that there was no significant difference between trophic groups in all three habitats

Table VII. - Mean density and biomass, SD in brackets, of the 8 most important species (overall rank index) on coral reefs (R), *Sargassum* beds (S) and *Halimeda* beds (H) habitats. First 8 species are those dominant on reefs. Next three species are those in the 8 dominant on *Sargassum* not included in the first 8 species and final eight species those dominant on *Halimeda* not included previously.

Species	Density (fish/m²)			Biomass (g/m²)			Rank (m²)		
	R (n =	S (n =	H (n =	C (n =	S (n =	H (n =	R	S	H
Neopomacentrus sp.	2.081 (2.385)	0.436 (0.744)	-	9.01 (15.84)	2.10 (13.71)	-	1	2	-
Pomacentrus moluccensis	0.24 (0.153)	0.167 (0.301)	< 0.001 (0.002)	1.33 (0.93)	0.96 (1.74)	0.002 (0.008)	2	1	77
Scolopsis bilineatus	0.048 (0.048)	0.011 (0.020)	-	6.36 (7.97)	1.31 (2.92)	-	3	4	-
Abudefduf sexfasciatus	0.149 (0.132)	0.036 (0.053)	-	2.42 (4.05)	0.65 (1.29)	-	4	8	-
Chromis viridis	2.00 (5.98)	0.029 (0.062)	0.011 (0.043)	8.92 (26.72)	0.11 (0.22)	0.01 (0.04)	5	29	29
Acanthurus nigrofuscus	0.031 (0.046)	0.010 (0.025)	-	2.69 (3.66)	0.64 (0.88)	-	6	10	-
Siganus doliatus	0.026 (0.026)	0.007 (0.013)	-	2.05 (2.33)	0.46 (0.91)	-	7	17	-
Abudefduf whitleyi	0.048 (0.086)	0.043 (0.041)	< 0.001 (0.001)	1.86 (2.60)	2.46 (5.48)	0.03 (0.11)	8	6	66
Acanthurus dussumieri	0.004 (0.005)	0.007 (0.010)	< 0.001 (0.001)	1.03 (2.08)	4.91 (9.39)	0.09 (0.27)	32	3	32
Scarus ghobban	0.006 (0.010)	0.005 (0.007)	0.001 (0.002)	0.85 (2.47)	3.68 (10.41)	0.62 (1.88)	20.5	5	9
Acanthurus blochii	0.013 (0.012)	0.007 (0.014)	< 0.001 (0.001)	1.56 (1.66)	0.94 (1.82)	0.02 (0.01)	10	7	89
Lethrinus genivittatus	-	0.002 (0.007)	0.032 (0.060)	-	0.07 (0.29)	0.96 (1.69)	-	90	1
Pomacentrus phillipinus	0.038 (0.033)	0.030 (0.042)	0.024 (0.060)	0.35 (0.29)	0.29 (0.43)	0.23 (0.60)	9	13	2
Dascyllus aruanus	0.077 (0.220)	0.020 (0.046)	0.025 (0.059)	0.50 (1.43)	0.12 (0.23)	0.13 (0.32)	29	22	3
Upeneus sp1	-	-	0.010 (0.039)	-	-	0.52 (1.88)	-	-	4
Upeneus tragula	0.001 (0.002)	0.001 (0.004)	0.004 (0.011)	0.19 (0.06)	0.10 (0.04)	0.120 (0.031)	82	88	5
Heniochus acuminatus	0.005 (0.016)	0.001 (0.003)	0.002 (0.003)	0.62 (2.27)	0.23 (0.56)	0.27 (0.73)	50	42.5	6
Parapercis cylindrica	0.002 (0.007)	0.003 (0.008)	0.005 (0.009)	0.03 (0.10)	0.07 (0.17)	0.07 (0.13)	98	73.5	7
Diagramma pictus	-	0.003 (0.009)	0.001 (0.004)	-	1.50 (4.31)	1.44 (4.62)	-	30	8

at the density level (Table XI). Another major feature of the covariance analyses is the absence of significant correlations between trophic groups and environmental variables for reefs and species richness, density and biomass, whereas significant correlations between trophic groups and environmental variables were the rule for *Sargassum* beds and *Halimeda* beds (Tables X, XI, XII). However, trophic groups were never strongly correlated ($p < 0.01$) to algal cover whichever habitat is considered.

Range of movement

In all three habitat types, species composition was dominated by sedentary and small radius roaming species, density by sedentary fish and biomass by small radius roaming fish (Table XIII). A χ^2 test (Table XIV) indicates that there was no difference in mobility structure at the species level between reefs and *Sargassum* beds and between *Sargassum* beds and *Halimeda* beds. All other comparisons between habitats were highly significant, in particular for density and biomass (Table XIV). In particular, the proportion of territorial fish (density and biomass) was greater on reefs than in algal beds. Conversely, density and biomass of large radius roaming fish as well as the density of small radius roaming fish, were lower on reefs than in the two other habitats.

MANOVAs indicate that the three habitats supported significantly different relationships between hard substratum or coral cover and overall mobility structures at the species level, but not at the density or biomass levels (Tables X, XI, XII). Conversely, MANOVAs indicate that for algal cover there was no difference in mobility structure at the species level between habitats, but significant differences at the density and biomass levels. No effect of year, distance to coast or depth on mobility structure was found when habitat was taken into account.

Table VIII. - Differences in trophic structure between habitats as determined by p values of a χ^2 test. NS: not significant.

	Reefs			Sargassum		
	Species	Density	Biomass	Species	Density	Biomass
Sargassum	NS	NS	NS			
Halimeda	0.00036	$< 10^{-5}$	$< 10^{-5}$	NS	$< 10^{-5}$	$< 10^{-5}$

Table IX. - Relative contribution of the different trophic groups to fish species composition, density and biomass on coral reefs (R), *Sargassum* beds (S) and *Halimeda* beds (H).

	Species (%)			Density (%)			Biomass (%)		
Category	R	S	H	R	S	H	R	S	H
Piscivores	5.9	7.6	11.1	3.6	4.8	5.1	17.8	13.9	9.3
Macrocarnivores	21.0	27.2	33.4	3.8	6.9	27.8	29.5	27.5	57.9
Microcarnivores	15.6	16.9	17.8	8.6	10.4	12.1	7.5	8.1	9.3
Zooplanktivores	15.9	14.9	19.0	65.4	52.6	43.4	20.9	19.1	7.5
Other planktivores	0.2	0	0	< 0.1	0	0	< 0.1	0	0
Macroherbivores	1.6	2.9	1.5	0.2	0.6	0.5	1	2.3	10.3
Microherbivores	25.2	21.8	13.5	14.1	19.8	10.1	19.3	25.1	5.6
Coral feeders	12.2	6.6	2.1	1.1	1.0	0.5	1.8	1.2	0.0
Detritus feeders	2.6	2.2	1.7	3	4.0	1.5	2.2	3.2	0.9

Table X. - Trophic and mobility composition in number of species per transect for the three habitats. The four first columns indicate the trophic and mobility composition in number of species per transect for the three habitats. The three last columns indicate the level of the MANOVAs for trophic and mobility structures respectively then the regression and covariance levels. ns: not significant; *: p < 0.05; **: p < 0.01; ***: p < 0.001.

Species/transect	Reef (R)	Sargassum beds (S)	Halimeda beds (H)	All sites (Σ)	Hard substratum Trophic *** Mobility *** R	S	H	Σ	Coral cover Trophic ns Mobility *** R	S	H	Σ	Algal cover Trophic ns Mobility ns R	S	H	Σ
Total	51.80	35.20	12.89	34.00												
Piscivores	3.05	2.67	1.43	2.41	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Macrocarnivores	10.88	9.58	4.31	8.39	ns	ns	**	*	ns	ns	**	ns	ns	ns	ns	ns
Microcarnivores	8.08	5.94	2.29	5.54	ns	***	***	ns	ns	*	ns	ns	ns	ns	ns	ns
Plankton feeders	8.22	5.23	2.45	5.40	ns	**	**	*	ns	*	ns	ns	ns	ns	ns	ns
Macroherbivores	0.81	1.03	0.19	0.69	ns	ns	***	ns	ns	ns	ns	**	ns	ns	ns	ns
Microherbivores	13.07	7.66	1.74	7.69	ns	**	***	**	ns	*	*	ns	ns	ns	ns	ns
Coral feeders	6.32	2.31	0.27	3.06	ns	***	***	***	ns	**	ns	***	ns	ns	ns	ns
Detritus feeders	1.34	0.78	0.22	0.80	ns	***	**	***	ns	**	ns	***	ns	ns	ns	ns
Territorial	5.60	2.60	1.28	3.22	ns	**	ns	ns	ns	*	*	ns	ns	ns	ns	ns
Sedentary	27.10	16.20	5.06	16.50	ns	***	***	**	ns	**	ns	ns	ns	ns	ns	ns
Roaming: small radius	15.85	12.15	4.28	10.98	ns	**	***	*	ns	***	ns	ns	ns	ns	ns	ns
Roaming: large radius	3.25	4.25	2.28	3.29	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns

MANOVAs. Regressions Reef (R), Sargassum (S), Halimeda (H); Covariance Analysis: (Σ).

Table XI. - Trophic and mobility composition in density (fish/m²) for the three habitats. The four first columns indicate the trophic and mobility composition in density (fish/m²) for the three habitats. The three last columns indicate the level of the MANOVAs for trophic and mobility structures respectively then the regression and covariance levels. ns: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Species/transect	Reef (R)	Sargassum beds (S)	Halimeda beds (H)	All sites (Σ)	Hard substratum Trophic ns — R	S	H	Σ	Mobility ns — R	S	H	Σ	Coral cover (MANOVAs) Trophic ns — R	S	H	Σ	Mobility ns — R	S	H	Σ	Algal cover Trophic ns — R	S	H	Σ	Mobility *** — R	S	H	Σ
Total	6.050	1.255	0.198	2.580									Regressions Reef (R), Sargassum (S), Halimeda (H); Covariance Analysis: (Σ)														
Piscivores	0.221	0.060	0.010	0.100	ns	*	*	ns	ns	*	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Macrocarnivores	0.229	0.087	0.055	0.126	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Microcarnivores	0.520	0.131	0.024	0.232	ns	**	*	ns	ns	**	ns	ns	*	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Plankton feeders	3.959	0.660	0.086	1.619	ns	***	***	ns	ns	***	ns	ns	*	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Macroherbivores	0.015	0.008	0.001	0.008	ns	ns	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Microherbivores	0.856	0.248	0.020	0.387	ns	**	**	ns	ns	**	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Coral feeders	0.066	0.012	0.001	0.027	ns	**	***	ns	ns	**	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Detritus feeders	0.183	0.050	0.003	0.081	ns	***	***	ns	ns	***	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	***	ns	ns	ns	***
Territorial	2.177	0.070	0.018	0.781	ns	**	ns	ns	ns	**	ns	ns	ns	**	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sedentary	3.396	0.930	0.102	1.523	ns	***	***	ns	ns	***	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	***	ns	ns	ns	***
Roaming: small radius	0.393	0.206	0.026	0.214	ns	*	***	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Roaming: large radius	0.084	0.045	0.050	0.060	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	***	ns	ns	ns	***

Table XII. - Trophic and mobility composition in biomass (g/m²) for the three habitats. The four first columns indicate the trophic and mobility composition in biomass (g/m²) for the three habitats. The three last columns indicate the level of the MANOVAs for trophic and mobility structures respectively then the regression and covariance levels. ns: not significant; *: p < 0.05; **: p < 0.01; ***: p < 0.001.

Species/transect	Reef (R)	Sargassum beds (S)	Halimeda beds (H)	All sites (Σ)	Hard substratum Trophic ns / Mobility ns				Coral cover Trophic ns / Mobility ns				Algal cover Trophic *** / Mobility ***			
					R	S	H	S	R	S	H	S	R	S	H	S
Total	103.9	34.6	10.7	51.1		Regressions Reef (R), Sargassum (S), Halimeda (H);				Covariance Analysis: (Σ)						
Piscivores	18.5	4.8	1.0	8.3	ns	*	***	ns	ns	**	ns	ns	ns	*	ns	***
Macrocarnivores	30.6	9.5	6.2	15.8	ns	**	***	ns	ns	*	ns	ns	ns	*	ns	ns
Microcarnivores	7.8	2.8	1.0	4.0	ns	**	***	ns	ns	*	ns	ns	ns	*	ns	ns
Plankton feeders	21.7	6.6	0.8	10.0	ns	**	***	ns	*	*	ns	ns	ns	ns	ns	ns
Macroherbivores	1.0	0.8	1.1	0.9	ns	*	***	ns	ns	ns	ns	ns	ns	ns	ns	ns
Microherbivores	20.1	8.7	0.6	10.1	ns	**	***	ns	ns	*	ns	ns	ns	*	ns	ns
Coral feeders	1.9	0.4	0.0	0.8	ns	**	***	ns	ns	*	ns	ns	ns	*	ns	ns
Detritus feeders	2.3	1.1	0.1	1.2	ns	***	***	ns	ns	*	ns	ns	ns	ns	ns	ns
Territorial	11.0	0.7	0.1	4.1	ns	***	ns	ns	*	**	**	ns	ns	ns	ns	ns
Sedentary	28.3	9.8	1.4	13.6	ns	**	***	ns	ns	*	ns	ns	ns	ns	ns	ns
Roaming: small radius	45.7	16.8	6.1	23.4	ns	**	***	ns	ns	*	ns	ns	ns	*	ns	ns
Roaming: large radius	18.9	7.0	3.1	9.9	ns	*	**	ns	ns	**	**	ns	ns	ns	ns	***

Covariance analyses (Tables X, XI, XII) indicate that there were differences between habitats in the relationships between hard substratum cover and species richness of sedentary and short ranging species. On the opposite, there were no difference at the density or biomass level. These analyses show also that there was no difference between habitats in the relationships between mobility groups with coral cover. At last, the relationship between long ranging species and algal cover was significantly different between habitats at the density and biomass levels.

DISCUSSION

The major question is to know if algal beds support specific fish assemblages and to understand the possible exchanges between these assemblages with those from adjacent reefs. Before these questions can be answered it is necessary to evaluate the study design and the consequences of the methods used.

Sampling design

The stations studied in this article were not performed according to a design which was initially intended for a comparison of fish assemblages among habitats. Therefore a number of questions may arise on the adequacy of this design to separate these assemblages and to minimize "ghost" variables (variables which effects can not be tested). The habitats were indeed significantly different for a number of time, space and environmental variables (Table I). The question was then to know if within an habitat the space and time variables changed the structure of the assemblages. The number of species affected (20 among 161 tested) was not very important and the contribution of these species to biomass was small (at most 20%). This is lower than findings in the same zone by Wantiez *et al.* (1996) or Kulbicki (1997). On the opposite, these species had at times contribution to total density up to 39% (Table IV). However, one should notice that most of these fish belonged to species which have high turnovers and which may be replaced by other spe-

Table XIII. - Relative contribution of the different ecological groups to fish species composition, density and biomass on coral reefs (R), *Sargassum* beds (S) and *Halimeda* beds (H).

Category	Species (%)			Density (%)			Biomass (%)		
	R	S	H	R	S	H	R	S	H
Territorial	10.8	7.4	9.9	36.0	5.6	9.1	10.6	2.0	0.9
Sedentary	52.3	46.0	39.3	56.1	74.1	51.5	27.2	28.3	13.1
Roaming: small	30.6	34.5	33.2	6.5	16.4	13.1	44.0	48.6	57.0
Roaming: large	6.3	12.1	17.7	1.4	3.6	25.3	18.2	20.2	29.0

Table XIV. - Differences in mobility structure between habitats as determined by p values of a χ^2 test. NS: not significant.

	Reefs			*Sargassum*		
	Species	Density	Biomass	Species	Density	Biomass
Sargassum	NS	$< 10^{-5}$	0.050			
Halimeda	0.00002	$< 10^{-5}$	0.00001	NS	$< 10^{-5}$	0.0041

cies with similar ecological traits. Such a replacement has been well illustrated on soft bottoms in New Caledonia (Wantiez, 1992a). Overall species richness, density or biomass were not influenced by time and little by space variables within an habitat (Table V). This latter result can be attributed to the little differences in distance to the coast between stations. Indeed, Grimaud and Kulbicki (1998) found that this distance is a major factor in defining the species composition and trophic structure of reef fish assemblages in the SW lagoon of New Caledonia. Similar findings exist for the Great Barrier Reef (Williams, 1982; Williams and Hatcher, 1983). However, the range of distances tested was much larger than in the present data set. At last, these changes in species composition within an habitat resulted in little changes of the trophic or mobility structures from one place to another or from one year to another. Such a stability within habitat of trophic or mobility structure has already been demonstrated by Kulbicki (1997) and several sets of data from New Caledonia, Tonga and French Polynesia currently under investigation show similar trends. For all these reasons, it seems reasonable to assume that time and spatial differences were not major factors in explaining differences in the fish assemblages in the present set of data.

The differences in species richness, density and biomass, as well as structure were essentially due to habitat and environmental variables. Among the latter, cover was measured with low accuracy methods. The magnitude of the differences of these variables between habitats makes however the separation between habitats unquestionable. On the opposite, small differences in cover within an habitat were not detected and therefore only the major effects of cover should be considered.

General habitat differences

This study demonstrates that important differences in species richness, density and biomass of fishes existed between macroalgal beds and coral reefs but also according to the type of algae. Whilst structural habitat complexity differences which exist between coral reefs and algal beds may probably explain the highest species richness and density of fish on reefs (more shelter by example), variations between *Sargassum* and *Halimeda* beds must be related to algal composition but also to general habitat characteristics such as substrate composition.

In a study of the fish assemblages of the Ouvea lagoon (Loyalty Islands), Kulbicki *et al.* (1994) observed significant correlations between fish species richness (but not density) and the proportion of rocky substrate and coral. In the present study, it is demonstrated that within an habitat several variables come simultaneously into play to explain the levels of species richness, density or biomass. These results suggest that substratum differences influenced fish distribution between algal beds. Whereas soft substrates were predominant in *Halimeda* beds and coral heads were rarely present, *Sargassum* was more associated with rocky substratum and coral (Table I). Such structures increased habitat complexity in *Sargassum* beds and allowed the presence of coral-associated species such as Chaetodontidae or provided shelter for small fishes such as Pomacentridae.

In addition to substrate differences, the percentage of algal cover was clearly higher in *Sargassum* beds than in *Halimeda* and, in spite of the absence of significant correlations within habitats, this factor could explain, at least partially, the highest fish abundance observed on *Sargassum* beds. In an experimental study on temperate reef fishes, Levin and Hay (1996) demonstrated that fish density increased with increasing *Sargassum* density. Moreover, at similar densities of algae, more fish were present on *Sargassum* than on other brown algae because *Sargassum* provided higher cover (greater

height of plants and biomass) than did the other algae. Similar correlations between vegetation cover, blade length or biomass and fish parameters have been observed in different aquatic environments (Stoner, 1983; Aliaume *et al.*, 1993; Pihl *et al.*, 1994) and have emphasised the influence of vegetation structure on fish assemblages.

Independent of the amount of vegetation cover, algal composition could influence fish distribution. Because of the existence of chemical and morphological (calcification) defences, *Halimeda* spp. appear to be some of the least preferred algae by herbivorous fishes (Hay, 1981; Littler *et al.*, 1983; Paul and Hay, 1986; Paul and Van Alstyne, 1988). Conversely, different studies have provided evidences that *Sargassum* are intensively grazed by fishes in some areas (Steinberg *et al.*, 1991; McCook, 1996). These observations are consistent with our results which show that the proportion of herbivorous fishes (mainly Acanthuridae and Siganidae) was low on *Halimeda* beds compared with *Sargassum*.

Composition of fish assemblages

Because of the existence of marked variations among samples within each habitat type, it was difficult to characterise fish species composition of the different habitats and especially on algal beds. Of a total of 202 and 86 species observed on *Sargassum* and *Halimeda* beds respectively, 83 and 49 species were present on only one transect and very few species occurred frequently. With the exception of two Pomacentridae (*Pomacentrus taeniometopon* and *Stegastes nigricans*) and two Chaetodontidae (*Chaetodon melannotus* and *C. trifascialis*) which were relatively common on reefs, most of the exclusive species were very scarce and could not be clearly associated with one habitat type. More generally, whereas clear differences in fish assemblages existed between coral reefs and *Halimeda* beds, there was a high overlap between some *Sargassum* samples and the other two habitats. Few important differences in species composition existed between reefs and *Sargassum* beds although abundance and occurrence were lower on *Sargassum*. On *Halimeda* beds, even the dominant species had relatively low abundance and occurrence. However, two of them, *Lethrinus genivittatus* and *Upeneus* sp. 1, seemed to be characteristic of this habitat type since they were absent or very scarce on reefs and *Sargassum* beds. Although *Lethrinus genivittatus* is known to be generally associated with vegetated areas (Randall *et al.*, 1997), the abundance of this species and several species of *Upeneus* on soft-bottom areas of the New Caledonia lagoon (Wantiez *et al.*, 1996) suggests that their presence on *Halimeda* beds was more related to substratum composition than to algae presence.

Additionally, if macroalgal beds play the same role for fishes as do seagrass beds, some species may only be present in this habitat at some periods of the year or occasionally for feeding. In the Caribbean Sea, Ogden (1980) and Baelde (1990) have established that fish mobility was a characteristic of seagrass bed fish assemblages which also seems to be the case on algal beds in New Caledonia since the proportion of roaming fishes was clearly higher on macroalgae than on reefs during our study.

Trophic structure and range of movement

In spite of a low similarity of fish species composition observed among habitat types and especially between reefs and *Halimeda* beds, both the trophic and ecological structure by species were relatively similar. The proportions of carnivores and coral feeders were significantly lower on *Halimeda* beds than on reefs. Coral cover and hard substratum covers had a significant influence on several trophic groups at the species level, whereas algal cover had no effect (Table X). In addition, on *Halimeda* beds most trophic

groups were highly correlated to hard substratum, whereas no such correlation was found on reefs (Table X). This suggests that on *Halimeda* beds, one of the major factor affecting trophic composition at the species level is hard substratum and not algae cover. Additionally, the trophic structures observed during our study were very similar to those observed by Kulbicki (1997) in different reefs and lagoon bottoms of New Caledonia. This suggests some constancy, at the species level, of the structure of fish assemblages.

For density and biomass, some of the observed variations between habitat types can be directly related to habitat characteristics. The large amount of sandy substrate on *Halimeda* beds appeared to be favourable to carnivorous fishes and especially to the sand-dwelling invertebrate feeders Lethrinidae and Mullidae (Harmelin-Vivien, 1979), the only families showing higher abundances than in the two other habitats. Conversely, because zooplanktivorous fishes have generally a small size (66% of fish density on reef but only 21% in biomass in our study) and are vulnerable to predation, most of them stay close to shelters provided by coral (Hobson, 1991). During our study, coral cover decreased from reef to *Sargassum* and *Halimeda* beds which was also the case for the proportion (in density) of zooplanktivorous fishes. In the same way, territorial or sedentary fishes (mainly small species staying near a shelter) were dominant on reefs whereas a higher proportion of the large roaming fishes was found on algal beds.

From the trophic and mobility structure data one may point out the major differences in the way these fish assemblages function. At the species level all three habitats have very close structures suggesting that they draw their recruits from the same species pool. On reefs and *Sargassum* beds most of the fish production is rather high and dominated by sedentary plankton feeders and small range herbivores, whilst on *Halimeda* beds production is much lower and linked to mobile carnivores. This is due to the abundance of shelters for the small plankton feeders and to the presence of hard substratum allowing the growth of microalgae for herbivores in the first two habitats. The contrast between shallow water *Sargassum* beds with large numbers of herbivores and deeper *Halimeda* beds dominated by carnivores is in some ways similar to the difference between shallow (0-10 m) seagrass beds in Mediterranean with abundant herbivores and deeper seagrass beds (10-30 m) dominated by carnivores (Harmelin-Vivien, 1983).

Possible exchanges between habitats

In the SW lagoon of New Caledonia reefs, *Sargassum* beds and *Halimeda* beds are often not far from one another and one may wonder if exchanges occur between these habitats. The overlap in species composition and the similitudes in trophic and mobility structures between reefs and *Sargassum* beds, the presence of high hard substratum and coral covers within *Sargassum* beds suggest that exchanges with reefs are very likely and could be extensive, especially for the largest species which roam over important ranges. On the opposite, direct exchanges between reefs and *Halimeda* beds are probably much more limited. The first reason is probably physical, *Halimeda* are much deeper and have little hard substratum or coral cover, two important components of reef habitat. However, exchanges probably do exist, in particular long ranging fishes such as Lethrinidae and Lutjanidae which are sheltered on reefs during the day may forage on *Halimeda* beds and soft bottoms at night, as suggested by Kulbicki *et al.* (1994) on Uvea Atoll. *Halimeda* beds could maybe play a role of reservoir for reef fishes, in the sense that a number of reef fish species are found in *Halimeda* beds, often associated to small rocks or coral heads. From there they may migrate to nearby reefs when conditions become suitable for their settlement. This type of interaction has been found in the Caribbean between reefs and a

number of nearby habitats (Parrish, 1989) and has been suggested between soft bottoms and reefs in New Caledonia by Wantiez (1992b). However, the very low densities on *Halimeda* beds and the low number of species in common with reefs suggest that these exchanges are probably of little significance for reefs. *Sargassum* beds are likely to play the role of a buffer zone between reefs and other habitats, in particular *Halimeda* beds. Their species composition, density and biomasses are indeed intermediate between those of reefs and *Halimeda* beds.

CONCLUSIONS

Our study gives a useful description of the poorly known fish assemblages that inhabit tropical algal beds and establishes a quantitative comparison with a well studied habitat type: coral reefs. It also demonstrates that different algal habitats support different fish assemblages as has been observed for seagrasses (Martin and Cooper, 1981; Stoner, 1983). However, more specific studies (i.e., comparison of similar areas with and without algae, spatial and temporal variations of fish assemblages associated with algal beds, comparison with seagrass beds, etc.) should be undertaken to determine the importance of this habitat for tropical fishes, especially for juveniles, as well as the possible interactions between algal beds and adjacent habitat such as coral reefs, mangroves or seagrass beds.

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